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Commentary

Are lakemounts hotspots of productivity and biodiversity?

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ABSTRACT

Oceanic seamounts are hotspots of biodiversity, productivity, and other ecosystem processes. Different hydrodynamic processes leading to physical-biological coupling dynamics occur in these systems making them oases in the open ocean. Due to their disproportional effects on ecosystem function (e.g., high biogeochemical rates), seamounts can also be considered ecosystem control points. On a smaller scale, abrupt offshore reefs in large lake ecosystems (i.e., "lakemounts") may serve similar roles as seamounts by parallel mechanisms. However, very little is known about lakemounts or the physical-biological coupling that could make these isolated habitats an important source of energy production and biodiversity for offshore, open-water regions of large lakes. We hypothesize that lakemount-induced upwellings serve a similarly important process in lakes as seamounts in the ocean, boosting productivity and biodiversity in offshore areas of large lakes. Identification of these biodiversity hotspots and ecosystem control points, and the mechanisms driving their processes, is vital for understanding how climate change may alter physical-biological coupling and resultant community- and ecosystem-level processes. Such linkages may play a key role for effective and cost-efficient environmental conservation and the maintenance of ecosystem function and services in large lake ecosystems in the face of global change.

1. Seamounts as hotspots of biodiversity

Oceanic seamounts rise over 1,000 m from the seafloor to within tens of meters of the surface. Their abrupt topography modifies hydrodynamics and interacts with surface wind action and water currents, leading to upwelling zones in the open ocean. These upwellings bring nutrient-enriched deep waters to the surface that support disproportionately high productivity, biomass, and biodiversity on and around the seamount, known as the "seamount effect" (Genin, 2004; Lavelle and Mohn, 2010; Leitner et al., 2020; Pitcher et al., 2007; Uda and Ishino, 1958; Box 1). Upwelling areas in the global ocean compose < 5 % of the oceanic areas but sustain > 20 % of the fishery captures in the world (FAO, 2022). By bringing cold and nutrient-rich water from pycnocline and below pycnocline to the euphotic zone, upwellings can enhance chlorophyll production up to 56 % at seamounts when compared to the adjacent open ocean, which promotes bottom-up effects through the entire food web (Leitner et al., 2020; Fig. 1).

Different processes other than upwelling also play a role in the high production observed around seamounts (e.g., Cascão et al., 2019; Domokos, 2022). For example, **topographic blockage** has been proposed as the cause of plankton aggregation around seamounts, which occurs due to the abrupt topographies that, in combination with

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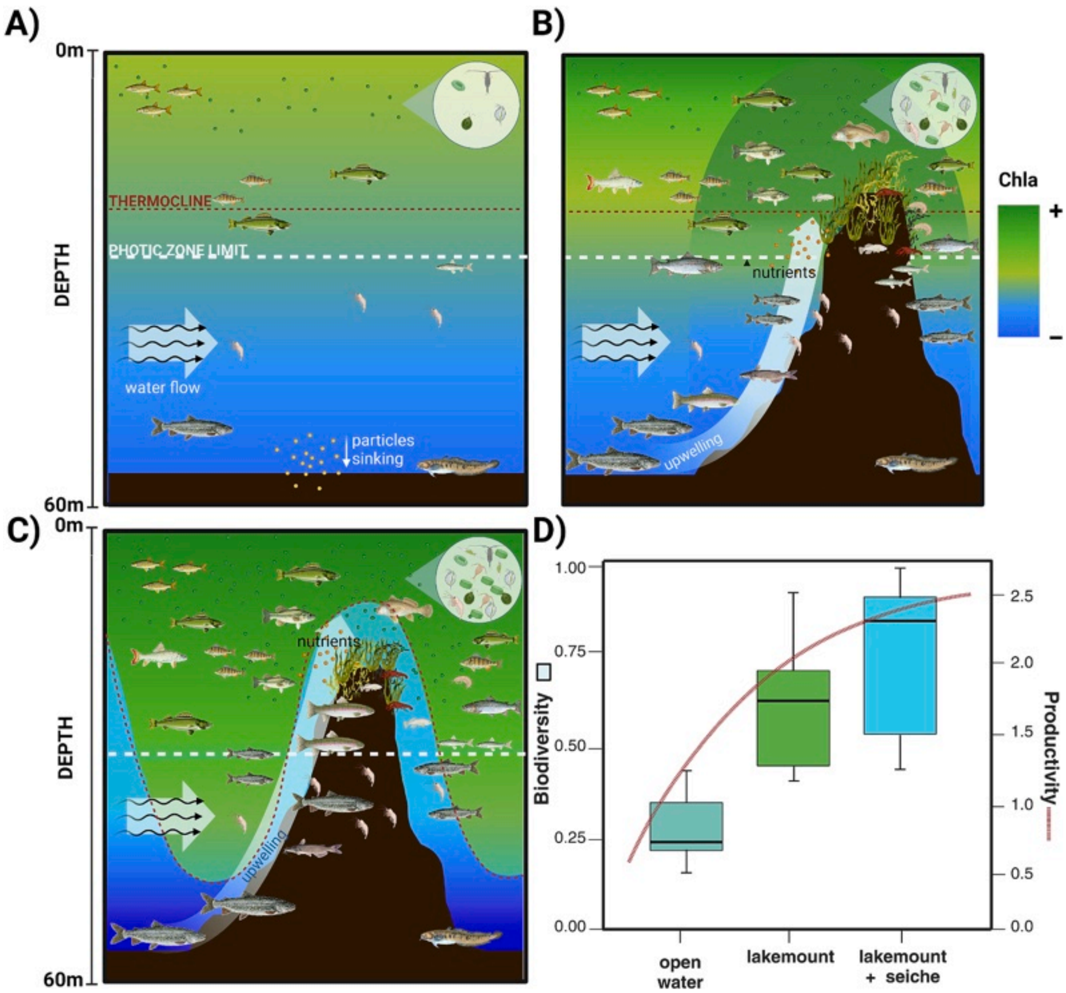
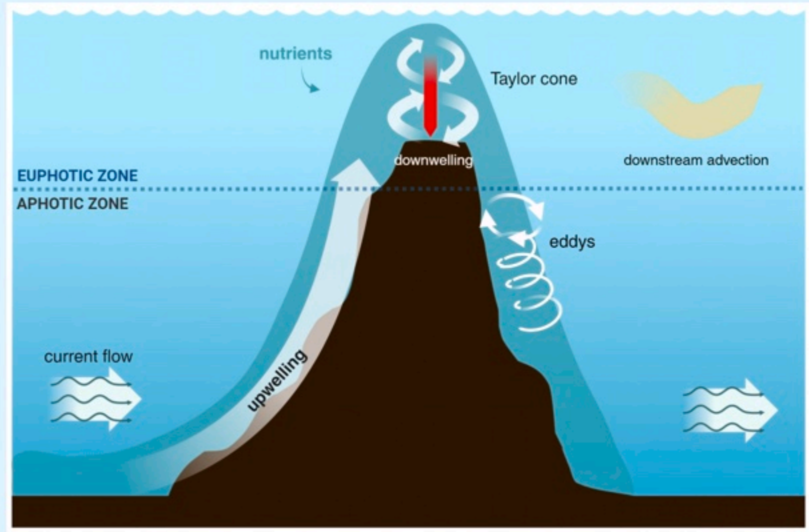


Fig. 1. Conceptual model of processes in deep lake habitats with and without abrupt offshore reefs ("lakemounts"). (A) Primary production is relatively low above the thermocline during stratified periods due to nutrient depletion in open-water habitats. (B) Primary production increases above the thermocline due to the presence of a lakemount that induces upwelling of nutrient-rich hypolimnetic waters. Lakemounts also support benthic primary producers by providing substrate in the euphotic zone, increasing the resources (e.g., habitat, food) available for primary and higher-level consumers, including fish. (C) Upwelling around lakemounts is intensified by internal seiches, which also mix the epilimnion and hypolimnion in the adjacent waters and produce a nutrient influx to shallower, photic-zone depths. (D) Hypothetical response of productivity (red dashed line) and biodiversity (boxplots) to the different habitats and conditions. Red dashed lines in A, B and C delimit thermocline depth and white dashed lines delineate the euphotic zone depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

advection and flow trapping (circular flow; Box 1), block and trap vertically migrant zooplankton in shallower waters during their migration downward deeper waters (Cascão et al., 2019; Genin, 2004). Seamounts also provide substrate for benthic organisms such as sponges, bivalves, crinoids, and corals (Samadi et al., 2007), which in turn attract fish (e.g., Campos et al., 2019; Du Preez et al., 2020; Kerry et al., 2022) and increase local biodiversity. Because seamounts can extend into the euphotic zone, they increase local taxonomic and functional richness by providing substrate for benthic producers, for example, and supply additional resources to upper trophic levels compared to open-water habitat (Leitner et al., 2020; Marchese, 2015). The effects of seamounts on ecosystem function make seamounts biodiversity hotspots and ecosystem control points in the open ocean (Bernhardt et al., 2017; Marchese, 2015; Box 1). Though analogous habitats exist in lakes, they have been largely overlooked. Steep reefs in large and deep lakes have the potential to act similarly to seamounts (i.e., "lakemounts"; Fig. 1A, B), disrupting water flow and promoting upwelling of deep, nutrient-rich water into the euphotic zone that fuels upper trophic levels. If lakemounts parallel the processes of oceanic seamounts, they could serve as key sites for biodiversity and productivity.

BOX 1. Concepts and definitions



Seamount effect: Subsurface effect generated by a combination of the abrupt topography of seamounts, oceanic circulation, and Earth's movement. When water currents reach a seamount slope, an upwelling of the deep, cold, and nutrient-rich waters reaches surficial ocean layers. Due to the Earth's rotation, a vorticity is formed in the upper layers on top of the seamount, forming a conical movement called "Taylor Cone", which reaches the euphotic zone and mixes the water layers. This mixing brings the cold nutrient-rich water into the euphotic zone, boosting primary productivity. Downwelling of the organic material occurs in the central part of the cone (red arrow), which provides resources to the benthic community on the seamounts. Source: Pitcher et al. (2007)

Hotspots in aquatic systems: Hotspots of biodiversity are usually identified as areas that contain relatively high numbers of species and endemism (e.g., the Amazon Forest or Madagascar). However, in aquatic systems hotspots can be challenging to define due to the dynamism of the environment and lack of distinct habitat borders. Generally, hotspots are areas with high ecological importance, including taxonomic and functional diversity and endemism. Aquatic hotspots are, therefore, areas with high biodiversity, productivity, trophic transfer, and physical-biological coupling processes. They can include distinct physical conditions that favor primary and secondary production, and promote aggregations of consumers (e.g., coral reefs). Source: Marchese (2015)

Ecosystem control points: Points in space and/or time that have high biogeochemical rates which alter the magnitude and timing of ecosystem fluxes, resulting in a disproportional effect on ecosystem processes (e.g., remineralization, denitrification). Examples of ecosystem control points are groundwater discharges (e.g., Briggs & Hare 2018) and hydrothermal vents. Source: Bernhardt et al. (2017)

Hot moments: Event or sequence of events with short-term duration that induces accelerated processes at a disproportionately high rate relative to the average rate and longer periods in the ecosystem. One example of a hot moment is a snowmelt event that rapidly delivers nutrients to the watershed. Source: Zhao et al. (2021)

Internal seiche: Internal waves formed when wind energy acting on the lake surface produces sufficient energy that exceeds water column stability. In thermally stratified water bodies, this energy applied to the differences in density of epilimnion and hypolimnion creates instability in the lower water layers. The wind pushes low-density epilimnetic water downwind, and an ascending movement of the hypolimnion occurs upwind, generating an internal wave. Source: Ostrovsky et al. (1996)

2. Lakemounts: What are they and what do we know?

Lakemounts are offshore natural reefs, spatially segregated from littoral habitats and associated effects of runoff, abundant shallow-water predators, and shoreline influences. They are locally known as "reefs" or "rock points" and are mapped on navigation charts and marked by buoys due to the sudden change in bathymetry that may represent navigational risks (Fig. 2, Box 2). We define lakemounts based on both their topography and their functional role, i.e., they have a base in the hypolimnion, an abrupt topography (greater than 4° or 7 % slope, similar to continental slopes) that changes hydrodynamic flow, likely promoting upwellings of nutrient-rich water from the hypolimnion, stimulating productivity, and creating biodiversity hotspots. The hard substrate offers a settling habitat for benthic producers and other sessile organisms, increasing local diversity, habitat complexity, and, ultimately, food resources (Box 2). For example, on lakemounts located in oligotrophic waters 27 to 77 km offshore in Lake Superior, dense and diverse communities of periphyton cover the rocky bottom, with the diatom community comprised of > 300 species (Edsall et al., 1991). This periphyton cover extends > 20 m below the surface, and this production may contribute significantly to the offshore food web (Edsall et al., 1991). Moreover, the aggregation of benthic organisms in these areas increases detritus production, which can be an important source supporting deepwater organisms that depend on this trophic pathway.

While nutrient-rich upwelling does not increase productivity in lakemounts below the euphotic zone, topographic blockage occurs on both deepwater and shallow mounts. Topographic blockage occurs when vertically migrating zooplankton, ichthyoplankton, and invertebrates such as mysids are advected by currents and trapped by lakemount topography during their dawn descent, making them vulnerable to predation during the day and providing resources to sustain fish populations (Houghton et al., 2010; Genin, 2004). Another important process in these areas is advection. Horizontal currents displace planktonic organisms and enhance fluxes of suspended particles at the bottom of topographic reliefs such as lakemounts to provide trophic subsides to growth and recruitment of benthic suspension feeders (Genin 2004). High concentrations of hydroids (Nalepa et al., 1987) and bivalves on the lakemounts at Lake Michigan Mid-Lake Reef Complex (MLRC), and sponges and bivalves in different lakemounts in Lake Champlain (personal observation; Box 2) support this idea. Ultimately, the mechanisms outlined here (upwelling, topographic blockage, provision of substrate and advection) are all likely involved in the aggregation of high production around lakemounts to varying degrees, and multiple mechanisms likely act together in these systems.

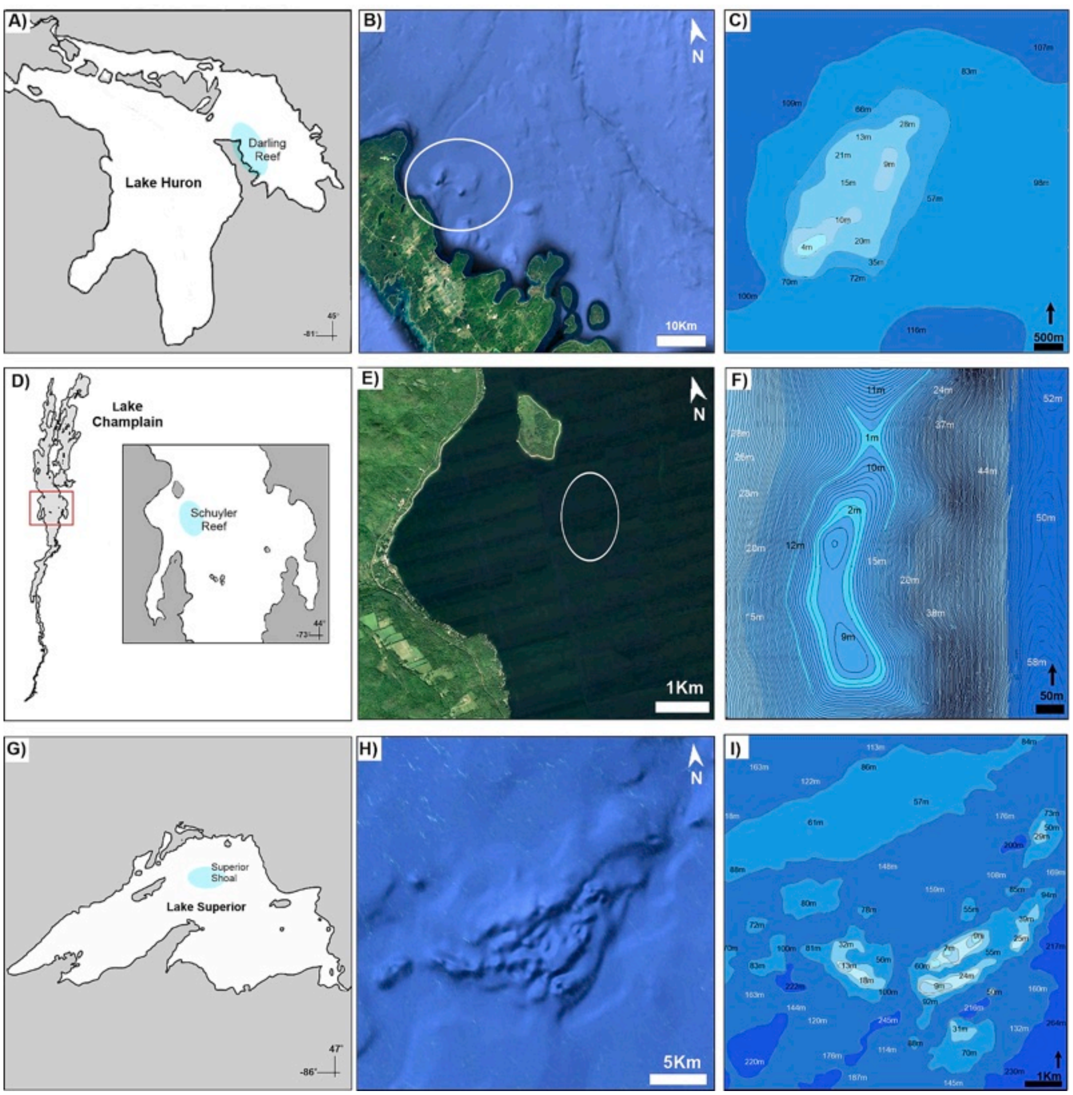


Fig. 2. Examples of lakemounts. A) Lake Huron, Canada; the area in blue shows the location of the lakemount Darling Reef, 6 km offshore. B) Topography (white circle indicates location of the reef) and C) bathymetry of Darling Reef (declivity 7.5°). D) Lake Champlain, United States, the area in blue indicates the location of the lakemount Schuyler Reef, 4–5 km offshore. E) Satellite image of Schuyler Reef location (white circle) and F) bathymetry of Schuyler Reef (declivity 8.6°) showing steep changes in depth around this lakemount. G) Lake Superior, Canada, the area in blue shows the location of Superior Shoal, 88 km offshore. H) Topography and I) bathymetry of Superior Shoal (declivity 10.7°). In figures C, F, and I lighter shades of blue indicate shallower depths and darker shades indicate deep areas. Arrows point to geographic North. Source images B, E, H: Google Earth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

BOX 2. Reefs, rock points, shoals, and lakemounts

As in oceans, large lakes present different geomorphic structures at the bottom that can be distinguished by composition, formation, and slope. Although various structures may be a risk for navigation, not all can be classified as "lakemounts". These structures in lakes can be defined:

Reefs and rock points: Aggregation of broken bedrock, solid bedrock, or bedrock ledges lying on the bottom of a lake that rise into the euphotic zone and potentially to the surface. Reefs provide substrate to a variety of organisms in the offshore area, such as freshwater sponges and aquatic vegetation. When these reefs are located offshore, have a steep slope and peak in the euphotic zone, we propose that the term "lakemounts" can be used. Lakemounts are a subset of reefs; not all reefs are lakemounts (A, below).

Reef complexes: group of summits at similar depths that comprise a reef, such as the Mid-Lake Reef Complex in Lake Michigan, or Superior Shoal in Lake Superior (Table 1).

Shoals: Elevation of the bottom that is constituted by unconsolidated material with a relatively shallow slope. Shoals do not produce the same hydrodynamic processes as lakemounts due to their soft bottom. Source: Collins 2011

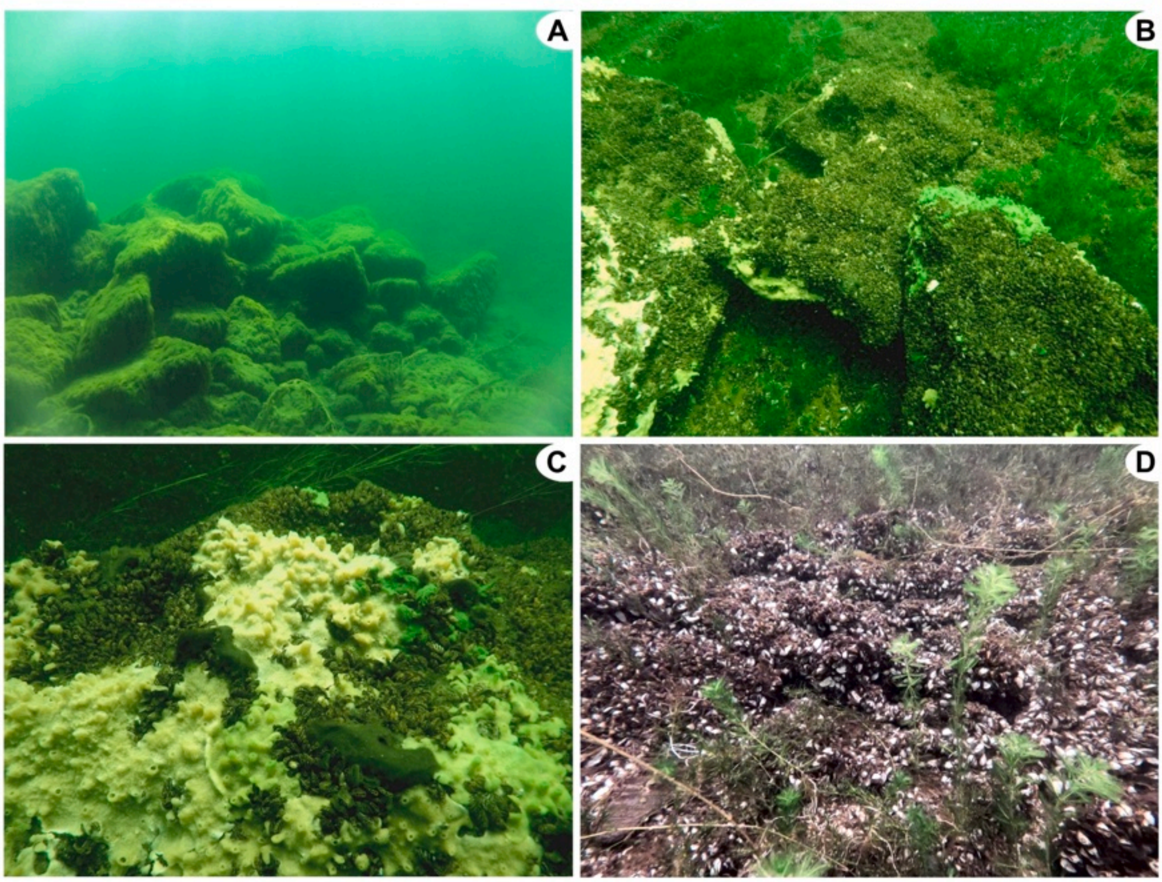


Illustration of contrasting reef types and summits: A) Reef (not lakemount) in Lake Huron, United States, covered by periphyton and filamentous algae (7 m). Lakemounts: B) mussels, plants, and C) sponges covering Ferris Rock at 10 m in Lake Champlain, United States; surrounding depths are 45 m. D) Zebra mussels (Dreissena polymorpha) and aquatic plants covering the summit (2 m depth) of Schuyler Reef at Lake Champlain. Depths adjacent to Ferris Rock and Schuyler Reef (within 3 km) drop to over 100 m. Photos: Ellen Marsden and Matthew Futia.

The Laurentian Great Lakes, for example, are large enough to have currents influenced by the Coriolis effect as in the oceanic gyres (Sterner et al., 2017; Box 1). Lake Michigan, which has northern and southern basins separated by the Mid-Lake Reef Complex, typically has cyclonic (i.e., counterclockwise) gyres in both the northern and southern basins with a clockwise current framing the MLRC (Beletsky and Schwab, 2001). These currents are a consequence of the interaction of wind driven currents, Coriolis effect, and bottom topography. Lake Superior also has strong currents with the Keweenaw Peninsula current the best studied (Bennington et al., 2010). Both the Lake Superior and Lake Michigan currents have consequences for larval fish dispersal because the currents are far stronger than larval fish swimming speeds (Beletsky et al., 2007, Oyadomari and Auer, 2008). Therefore, hydrodynamics in the Laurentian Great Lakes create physical-biological interactions, and when these currents intercept “abrupt topographies” such as the MLRC, they likely undergo similar processes observed at seamounts (Genin, 2004; Isaacs and Schwartzlose, 1965; Ullman et al., 1998), creating upwelling zones. In temperate lakes, nutrients are taken up rapidly and converted to phytoplankton biomass in the epilimnion (Fig. 1A), then transferred up the food web and recycled via egestion, excretion and decomposition or lost to the bottom through sedimentation (Sommer et al., 2012). This process leads to nutrient limitation in surface waters, especially during the summer (Ostrovsky et al., 1996). Consequently, upwelling of nutrient-rich hypolimnetic water around lakemounts may provide an important subsidy to primary and secondary productivity and subsequent support and maintenance of fish populations and fisheries in oligo- and mesotrophic systems (Fig. 1B), as in the ocean (Calil and Richards, 2010; Leitner et al., 2020; White et al., 2007). In lakes, most studies of upwelling are focused on climatic events (e.g., Troitskaya et al., 2015), internal seiches (e.g., Brooks et al., 2022; Hamblin et al., 2003), or coastal upwelling (e.g., Csanady, 1977; Haffner et al., 1984; Rowe et al., 2019). The investigation of lakemounts/topographic relief-related upwellings, linked to other hydrodynamic processes, is missing in large freshwater ecosystems and may represent an important discovery to understand lake ecosystem functioning, biodiversity hotspots, and priority habitats supporting lake ecosystem health and services.

Similar to currents, internal seiches (Box 1) have the potential to upwell nutrient-rich hypolimnetic water to the thermocline in stratified lakes during summer months (Flood et al., 2020; Ostrovsky et al., 1996; Fig. 1C). High frequency internal waves are detected at slope boundaries, and the influence of these seiches can change the bottom temperature as much as 10 °C (Lorke, 2007). When a seiche interacts with the topography of lakemounts, we expect the upwelling can be intensified similar to events at seamounts (Gove et al., 2016; Leitner et al., 2020) and the input of hypolimnetic nutrients into the euphotic zone can temporarily boost productivity on and around lakemounts during such “hot moments” (Box 1; Fig. 1D). Preliminary work at Schuyler Reef, in Lake Champlain (United States), detected consistent upwellings around this lakemount during summer months (thermally stratified period), and occasions where hypolimnetic water reached the epilimnion at 10 m depth, highly related to internal seiche occurrences.

The enhancement of productivity and consequently of the entire food web that occurs on seamounts is stronger in the tropics than in temperate latitudes due to the stronger thermal stratification of the water column, which leads to internal seiches (Box 1). In lakes, however, thermal stratification has different latitudinal trends than the ocean due to differences in the water column depth, being common in temperate regions due to the shallower water column compared to the open ocean. Deep tropical lakes such as the African Great Lakes (e.g., Malawi, Tanganyika; average depth > 200 m) have a permanent thermal stratification, thus creating an anoxic hypolimnion nearly devoid of animal life (Fryer and Iles 1972, McKinnen, 2023), while shallower tropical lakes (e.g., Lake Nicaragua, Lake Albert; average depth < 25 m) may present a weak or absent stratification (Cole 1976, Talling 1963). The thermal stratification observed in shallow tropical lakes is mostly short-term, and with a smooth gradient, with stratification formed in surficial layers during the day due to solar radiation and disrupted by evaporative heat losses at night (Baxter et al., 1965). Temperate lakes have a much longer and stronger thermal stratification period, usually starting in late spring and remaining until early fall. In this 3–4-month period, seiche events may occur frequently and mix water layers, boosting production in surficial layers over several days. Therefore, the frequency of hot moments around lakemounts is expected to have an opposite latitudinal trend compared to seamounts, because lakes in tropical and subtropical latitudes are either permanent or weakly (or not at all) thermally stratified, and temperate lakes have a strong and seasonal stratified period.

To date, only three published studies have applied the concept of oceanic seamounts to lakes. The first examined lake trout (*Salvelinus namaycush*) spawning locations in Lake Michigan (United States) and discovered that steep reefs in deep waters are preferred spawning areas, concentrating spawning fish and providing prey resources for their offspring (Janssen et al., 2006). The second study, also about a lakemount of Lake Michigan, demonstrated “topographic blockage” in vertically migrating zooplankton, making the zooplankton vulnerable to predation during the day and a possible mechanism to sustain fish populations (Houghton et al., 2010). The last study demonstrated the importance of lakemounts in Lake Superior (United States) as offshore sites that provide protection, food, resources, and preferred habitat for a diversity of lake trout ecotypes, attracting genetic diversity to sustain diverse lake trout populations (Sitar, 2023). All three studies described lakemounts as important habitats for a single top predator species and highlighted the importance of these habitats for fisheries management. What is lacking, however, are broader studies that address the greater ecosystem roles of lakemounts, including the processes that promote apparently preferred use of these habitats by certain species, and ultimately the potential function of lakemounts as ecosystem control points and biological hotspots.

3. Lakemounts and seamounts: Parallel processes at different scales

Comparison of the impacts of seamounts and lakemounts is challenging because neither have been well catalogued, and the magnitude of their effect on their respective ecosystems is scaled by the depth and volume of the surrounding waters. Seamounts rise > 1,000 m from the sea floor and may extend over 500 km^2 (Harris et al., 2014; Leitner et al., 2020; Pitcher et al., 2007). In contrast, known lakemounts are relatively small but appear to generate similar effects on surrounding hydrodynamics (Beletsky and Schwab, 2001; Cuhel and Aguilar, 2013; Isaacs and Schwartzlose, 1965; Ullman et al., 1998). Their areas are variable, from 4 to > 2,800 km^2 and rising from dozens to hundreds of meters depth (Fig. 2; Table 1). Another critical difference between seamounts and lakemounts is their steepness. Seamounts have a slope of ~ 17° (Du et al., 2020; Pitcher et al., 2007; Smith, 1988) and can be even steeper near the summit (around 35°; Smith, 1988). Lakemounts, comparatively, tend to have shallower slopes (e.g., 8.6° Schuyler Reef in Lake Champlain, 7.5° Darling Reef in Lake Huron).

An important factor in generating a “seamount effect” is the influence of Earth’s rotation (Box 1). Though detectable in large lakes, the influence of the Coriolis effect on water circulation is much smaller compared to the open ocean, and lakemounts typically have shallower summits (e.g., 2–8 m from the surface vs. 30 m at Gorringe Seamount or 150 m at Great Meteor Seamount, Atlantic Ocean). Therefore, upwelling likely extends vertically into the surficial waters of lakemounts even without the Taylor Cone formation commonly observed at seamounts (Box 1), but the horizontal extension of the “lakemount effect” (i.e., plume effect) may be smaller around lakemounts than seamounts (Galbraith et al., 2023; Leitner et al., 2020; Pitcher et al., 2007). In large lakemount systems, such as the MLRC (Lake Michigan), seamount-like upwellings that mix nutrients at the surficial waters and Taylor Cones

Table 1
Characteristics of some lakemounts of the Laurentian Great Lakes and Lake Champlain, Canada and United States. "Slope" is calculated by the rise of the mount (depth from foot to summit) divided by the run (distance between foot and summit), portraying an average for the mount. Slope is provided in degrees and percent (°; %). A 100% slope is equivalent to 45°. "% of lake" refers to the percentage of the lake area that the lakemount covers.

Lake	Reef	Slope	Reef area (km^2)	Surrounding depth (m)	Summit depth (m)	Lake area (km^2)	% of lake
Michigan	Sheboygan Reef *	4.6°; 8.0 %	580	80	38.0	57,800	1.00
Huron	Darling Reef	7.5°; 13.2 %	18	80	4.0	59,600	0.03
Superior	Superior Shoal**	10.7°; 18.9 %	52	236	6.4	82,100	0.06
Superior	Stannard Rock	4.3°; 7.5 %	< 20	100	5.0	82,100	0.02
Champlain	Schuyler Reef	8.6°; 15.1 %	4	49	2.0	1,269	0.32

* Sheboygan Reef is part of the Mid-Lake Reef Complex (MLRC)
**Local names frequently do not accurately define geological features. Superior Shoal is formed by four ridges of basaltic rocks and is technically a reef complex (see Box 2).

downwelling have been suggested as processes supplying resources to filter-feeders at the bottom of the reefs (Cuhel and Aguilar, 2013), but these mechanisms may not be present at smaller and shallower lakemounts. Although the scale of hydrodynamic processes generated by lakemounts is smaller and more localized than seamounts, the volumes of water in lakes are similarly orders of magnitude smaller than in oceans, suggesting the hypothesis that lakemounts likely have a significant impact on lake ecosystems when present. To illustrate the point, an individual seamount may only represent 0.001 % of the Atlantic Ocean area, whereas lakemounts can encompass 1 % of a lake's area (e.g., Sheboygan Reef, Lake Michigan; Table 1). Given the relative ratio of area covered by lakemounts compared with seamounts (Table 1), their potential influence on lake ecosystems may be important.

Pinnacle reefs are offshore reefs in marine systems that demonstrate the importance of processes at smaller scales. They have a steep "seamount" shape but are smaller than seamounts in height and extension (Galbraith et al., 2023). In these areas, hydrodynamic processes influence higher fish abundance, biomass, and richness compared to emergent offshore and nearshore reefs (Galbraith et al., 2023). Near pinnacle reefs, currents are faster and more variable in direction due to the topographic relief, affecting different processes around the reefs and making them biological hotspots even when compared to other highly diverse coral reef systems (Galbraith et al., 2023). Another parallel in a very different system is the Akademicheskii Ridge in Lake Baikal (Russia). This ridge has a volcanic origin and separates the lake into different basins. Due to the accentuated relief of this ridge, pelagic upwellings recorded in the area can last for 35 days on average (Shimaraev et al., 2012). The bottom of the Akademicheskii Ridge is rich in organic matter and biological activity (Khanaeva et al., 2010; Pavlova et al., 2019), and the high biodiversity found around this area (Sideleva, 2003) is likely due to these physical-biological processes as a result of the topographic relief. Such evidence suggests that lakemounts, although smaller scale than oceanic seamounts, can generate physical-biological processes parallel to seamounts.

4. Climate change: Possible impacts on lakemounts

Wind plays a critical role in driving upwellings and internal seiches through its influence on water currents and subsequent interactions with the steep slopes of seamounts (Aguirre et al., 2019; Leitner et al., 2020). Climate change is affecting the speed and direction of winds worldwide, and thus directly influences coastal upwelling intensity and internal seiche frequency (Aguirre et al., 2019; Eichelberger et al., 2008; Ostrovsky et al., 1996; Woolway et al., 2020). Additionally, the duration of thermal stratification in lakes has been increasing due to global warming, and under a high greenhouse gas emission scenario we can expect the stratified period in Northern Hemisphere to increase by > 30 days this century (Woolway et al., 2021a). Therefore, upwellings may become more frequent and intense around lakemount areas with climate change, and the frequency of internal seiches may increase due to the increase in wind speed in some parts of the world, as a consequence of lengthening of the thermal stratified period.

Global warming will also lead to stronger stratification and reduced mixing in lakes because warmer water in the epilimnion will result in a larger density difference between hypolimnetic and epilimnetic water. Therefore, more energy will be needed to mix nutrients from the hypolimnion into the euphotic zone and supply primary productivity (Kraemer et al., 2015; Kraemer et al., 2022; Woolway et al., 2021a), resulting in decreased primary productivity in offshore areas. Observations from 23 years of satellite data revealed that 65 % of investigated lakes worldwide presented a trend of increasing chlorophyll-a (proxy for phytoplankton) due to anthropogenic-induced eutrophication (e.g., agriculture activity, sewage, etc.), while many other lakes (35 %) experienced a decrease in phytoplankton due to effects of climate change (Kraemer et al., 2022). These climate change effects include changes in hydrological and mixing regimes that are reducing nutrient inputs and, consequently, decreasing phytoplankton production (Kraemer et al., 2022). In this climate change scenario, lakemounts may be an important oasis for biodiversity and productivity because the frequency and seasonal duration of upwelling that fertilizes epilimnetic waters may increase, thereby intensifying the occurrence of hot moments (Box 1), providing a supply of nutrient-rich hypolimnetic waters to an increasingly nutrient-limited euphotic zone and fueling primary producers and consequently higher trophic level consumers (Fig. 1C). Consequently, the combination of wind energy and topographic upwelling may be fundamental to boost productivity in stratified lakes during summer, and lakemounts may serve as critical habitat for conservation that could play important roles for the maintenance of lake ecosystem functioning under a changing climate.

5. Perspective: Studying lakemounts

The dynamic nature of aquatic systems has prompted aquatic scientists to define hotspots as areas with significant ecological importance, including high biodiversity, productivity, trophic transfer, and physical-biological coupling processes (Hazen et al., 2013; Marchese, 2015; Palacios et al., 2006). We posit that more intensive study of lakemounts is needed and is a key component of identifying hotspots and hot moments in lakes. Environmental predictors such as bathymetry, shelf-breaks, water surface temperature, chlorophyll-a, and others should be evaluated to identify their potential to identify and explain the spatial distribution and persistence of such hotspots (Gove et al., 2016; Marchese, 2015). One of the primary biological indicators that is easily measurable and an indicator of biological hotspots in aquatic systems is chlorophyll-a concentration, a proxy for primary productivity (Marchese, 2015; Papenfus et al., 2020). Satellite-derived chlorophyll-a and surface water temperature data have been used to evaluate the persistence of chlorophyll-a enhancements, frequency of upwellings, and the relationship with fishery harvests around seamounts and islands (Gove et al., 2016; Leitner et al., 2020). Similarly, surface temperature and chlorophyll-a data derived from remote sensing have been used to evaluate changes in lake temperature and mixing regimes and to show the effects of climate change in lake primary productivity around the globe over time (Free et al., 2022; Kraemer et al., 2022; Woolway and

Merchant, 2019; Woolway et al., 2021b). The use of these kinds of data provides an opportunity to evaluate lakemounts as analogues to seamounts.

In marine systems, seamounts are recognized as biological hotspots and ecosystem control points where physical-biological coupling plays a key role. In marine offshore reefs, for example, hydrodynamics and topography play a fundamental role in describing fish abundance, biomass, and diversity (Galbraith et al., 2023; Gove et al., 2016). Focused lakemount studies that integrate physical, chemical, and biological processes can provide fundamental information on these potentially important habitats for ecosystem-based management. Models predicting the effects of climate change in ecosystems do not include these biophysical processes occurring in seamounts, lakemounts, and offshore reefs (Gove et al., 2016), and they may be important habitats currently supporting ecosystems' function. Therefore, physical-biological coupling processes must be considered in modeling efforts to predict the future of aquatic systems in the face of global change (Gove et al., 2016). Global climate change is negatively affecting biodiversity worldwide, and environmental policies and conservation efforts must focus on biological hotspots because they harbor high diversity and important ecosystem processes in a relatively small habitat. Identification of such hotspots is fundamental for effective and cost-efficient environmental conservation (Gove et al., 2016; Marchese, 2015) and the maintenance of ecosystem function and services in face of the global change threats.

CRediT authorship contribution statement

Bianca Possamai: Writing – review & editing, Writing – original draft, Visualization, Project administration, Data curation, Conceptualization. **J. Ellen Marsden:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **John Janssen:** Writing – review & editing, Conceptualization. **Michael D. Rennie:** Writing – review & editing, Conceptualization. **Thomas R. Hrabik:** Writing – review & editing, Conceptualization. **Jason D. Stockwell:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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